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THE STRUCTURE AND RELATIONSHIPS OF THE AMERICAN PELYCOSAURIA.

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PERHAPS the greatest interest excited in the morphology of the Permian reptiles of the order Pelycosauria centers about the development of the temporal and quadrate regions as they seem at present to afford the most direct phylogenetic evidence of the origin of the mammals. The fragmentary character of the specimens and the character of the matrix in which they are preserved has rendered advance in the knowledge of the group very slow. In previous papers, both alone and in collaboration with the late Dr. Baur, the author has made known some of the structures of the order, has demonstrated its Rhyncocephalian nature and has given a new definition (Baur and Case '97 and '99). These conclusions were based upon new material, but affected seriously the work of Cope; they were accepted by Cope for but one of his forms only (Diopeus leptocephalus) with the proof that he had already recognized the character in that form (Cope '97). The unfortunate death of Prof. Cope rendered the type specimens temporarily unavailable so that continued study was almost impossible, but the collections have since come into the possession of the American Museum of Natural History in New York, and through the kindness of the Director of the Department of Paleontology the author was permitted to examine the types during the past summer. As the material was made available to me even before cataloging by the Museum, I desire to express my thanks publicly to Dr. H. F. Osborn for his kindness in the matter.

Unfortunately the most of the type specimens have never been freed from the matrix, Prof. Cope contenting himself with the description of new forms and such characters as could be made out from the uncleaned specimens. A reëxamination of the types in the light of better preserved and prepared material has led me to conclusions very different from those of Cope and of far-reaching effect upon the classification of the Pelycosauria and the related Permian reptiles of other countries.

These conclusions may be stated as follows: —

1. All known reptiles from the American Permian, other than the Cotylosauria, possessed two temporal arches; there is no approach to a single zygomatic arch, as described by Cope in some of them.

2. The Pelycosauria followed a line of development that led to extinction while the persistent line of development was followed in other regions, perhaps in Africa. The progress of development, from a stage represented by Diopeus, is expressed in the skull as follows: —

(a) The depression of the posterior angles of the skull (suspensorial region) by the shortening and degeneration of the quadrate; the bones of the temporal arches remaining distinct but becoming very slender. This process leading to extinction by the weakening of the articular region.

(b) The gradual elevation of the facial region of the skull and the lessening of the transverse diameter through the vertical growth of the maxillary and the narrowing of the frontals and nasals.

(c) The increase in size of the maxillary and premaxillary tusks, the deepening of the diastema, the increasing convexity of the alveolar edge and the development of serrations on the edges of the teeth.

(d) The increase in size of the ectopterygoid process of the pterygoid bone.

(e) Correlated with these changes the development of the enormously elevated neural spines.

Following is a short description of the skulls of the types representing the advancing stages of the development. The genera Dimetrodon, Embolophorus, and Naosaurus are not described, as the first two have been very fully described (Baur and Case '99 and Case[1]) and Naosaurus is very similar to them in the regions under discussion.

Theropleura uniformis. — Only the portion of the skull anterior to the posterior edge of the orbits is preserved; but this much is fairly free from the matrix, and the parts are easily made out. A careful examination of the skull compels me to differ from the description by Cope in one or two points. He mentions (Cope '80) the presence of "at least one large incisor tooth," and says the incisor teeth are separated from the maxillary teeth by a diastema. The anterior end of the snout is crushed, but the incisor teeth are seemingly all preserved, and I could not detect any one that was notably larger than the others; they are small and sharply recurved. Neither could I detect the presence of a diastema marked by any concavity of the alveolar edge of the maxillary bone such as is so persistent in the other American Pelycosauria; it is possible that there was a lack of teeth at this point, but as the bone is somewhat crushed at the point it is impossible to say certainly. As mentioned by Cope, there is no distinct maxillary canine, but the teeth increase in size to near the middle of the series and then diminish so that the 19 from the posterior end is the largest; the whole tooth line and the alveolar edge of the maxillary is straight without a trace of the convexity downward that marks the more specialized form. As described by Cope, the skull is low and acuminate; the orbits are large and the nares are near the anterior end of the snout on the sides. The whole skull is strikingly similar in general outline and appearance to the skull of Proterosaurus, and in just the same characters of a low and broad skull it differs from the specialized Pelycosauria. As the posterior portion of the skull is destroyed it is impossible to say with absolute certainty what was the condition of the temporal arches, but from the other relations of the skull there seems no reasonable doubt that they were as in Proterosaurus, *i.e.*, with two distinct arches.

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[1] A description of *Embolophorus dollovianus*, unfortunately delayed will appear in the Journal of Geology for January and February, 1903.

Cope describes the neural spines as elevated in all the species of Theropleura, but this is not to be taken in same sense as the elevation of the spines in the specialized members of the Pelycosauria. The length of the elevated spines does not exceed two or three times the length of the centrum where in Dimetrodon it is as much as 28 times the length of its centrum.

Diopeus leptocephalus. — The skull of this form is represented by disarticulated fragments which are fortunately quite free from crushing, and from the matrix. The fragment showing the temporal region is made up of the quadrate and quadrato-jugal, the united squamosal and prosquamosal; cemented to these are the pterygoid and the epipterygoid almost in the natural position. These fragments show that the temporal region, as figured by Cope (Cope' 92), was very similar to the same region in Sphenodon which it especially resembles in the united squamosal and prosquamosal. The anterior end of the prosquamosal is missing, but the squamosal is complete and shows the articular surface for the parietal. The posterior edges of the temporal vacuities are preserved and show that they were wide open and somewhat oval as represented in figure 1.

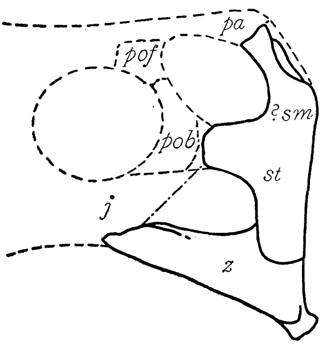

FIG. 1. Temporal region of Diopeus leptocephalus. *pa*, parietal; *pof*, postfrontal; *pob*, postorbital; *? sm* (squamosal) supramastoid; *st*, (prosquamosal) supratemporal; *j*, jugal; *z*, (quadrato-jugal) zygoma. After Cope.

The resemblance to the quadrate region of Sphenodon is somewhat superficial as the quadrate does not appear on the lateral surface but is covered by the vertical extension of the quadrato-jugal. The quadrato-jugal is much stronger than in Sphenodon and has the form of a right angle with one arm vertical and the other extending horizontally forward. The vertical arm overlaps the outer surface of the quadrate as described and meets the squamosal, the horizontal arm joins the jugal and forms with it a strong inferior bar. Seen from the rear it is evident that the squamosal comes down as far as the lower limit of the quadrate and appears on the outer surface of that bone. The pterygoid comes well up on the inner surface so that the quadrate is practically surrounded by bones and has relatively small vertical extent. Figure 2.

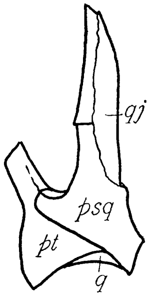

Fig. 2. Posterior view of temporal region of Diopeus leptocephalus. *gj*, quadrato-jugal; *psq*, prosquamosal; *pt*, pterygoid; *q*, quadrate.

The facial portion of the skull is formed almost entirely by the maxillary which presents some peculiarities. It is relatively long and the alveolar edge is almost straight with hardly a trace of the sharp downward convexity of the specialized Pelycosauria. On the inner side of the maxillary the lower edge is locally thickened by the development of a sharp buttress which accommodates the roots of the teeth; near the anterior end of the maxillary there is a single greatly enlarged canine and the buttress is correspondingly enlarged but no where near so much as in the most specialized forms of Dimetrodon, instead there is a strong rib developed on the lower side of the maxillary from the base of the root of the tooth to the top of the maxillary bone. The root does not extend into the bone as far as in Dimetrodon. This maxillary canine is rather more posterior in position than in Dimetrodon, posterior to it are 19 counted teeth and alveoli, but a portion of the bone is covered by a fragment of the lower jaw so that there were probably from 23 to 25 teeth; anterior to the canine are four teeth and alveoli in the maxillary. Where the maxillary meets the premaxillary there is a shallow depression of considerable antero-posterior extent, but it is lined with teeth throughout so that it is but the beginning of a diastema.

The form of the premaxillary is quite similar to that of Dimetrodon, there is a vertical anterior process which forms the anterior edge of the nares. There is but a single large incisor which is the first or inner one and posterior to it there are four much smaller.

Another fragment shows the upper portion of the maxillary and the frontal united by their inner surfaces. The two portions of the maxillary show that it was a thin, elevated plate, but relatively not nearly so high as in Dimetrodon. The frontal differs markedly from the frontal of Dimetrodon and all the specialized Pelycosauria, it is nearly as broad as long, showing that the top of the head was flat and broad. The orbital region is not preserved, but the anterior portion of the preorbital is, and this with the posterior end of the maxillary serves to locate its position with fair accuracy. The front edge of the preorbital is marked by the edge of a pit or foramen which is similar to the pits described by Seeley in Cynognathus and regarded by him as harboring a gland. In figure 3 is shown a partial restoration of the skull of Diopeus illustrating the beginnings of the features found in the more specialized Pelycosauria.

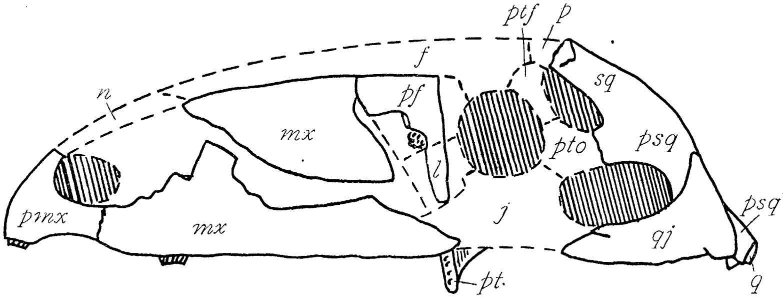

FIG. 3. Restoration of skull of Diopeus leptocephalus. *n*, nasal; *pmx*, premaxillary; *mx*. maxillary; *f*, frontal; *pf*, prefrontal; *l*, lachrymal; *j*, jugal; *pt*, pterygoid; *ptf*, postfrontal; *pto*, postorbital; *p*, parietal; *sq*, squamosal; *psq*, prosquamosal; *qj*, quadrato-jugal; *q*, quadrate.

The pterygoid bone is also interesting as showing the simple beginnings of the peculiar pterygoid characteristic of the Pelycosauria. There is the same tripartite division of the bone, but in the Dimetrodonts the posterior limb extends only as far back as the quadrate and is united with it by cartilage while in Diopeus it articulates strongly with the quadrate. The middle line is destroyed but the external or ectopterygoid process is much more slender and thin than the same process in the Dimetrodonts. The outer surface which abuts against the lower jaw is slightly rugose and the lower edge carries 15 teeth and alveoli.

In Sphenodon there is the same ectopterygoid process but is smaller and perhaps does not touch the lower jaw; it is made up of the pterygoid and ectopterygoid but in the Pelycosauria there is no distinct ectopterygoid that I have ever seen, it is either closely co-ossified with the pterygoid or is between the anterior plate of the pterygoid and the maxillary, a region not preserved in any known specimen. Seeley describes a similar process in the African Theriodonts but says it is made up of the ectopterygoid and palatine.

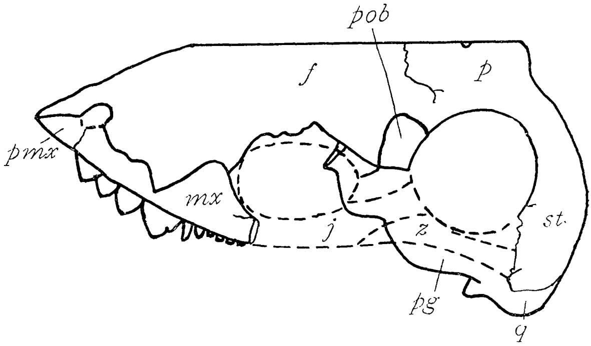

FIG. 4. Edaphosaurus pogonias. Side and top view of crushed skull. *pmx*, premaxillary; *mx*, maxillary; *f*, frontal; *j*, jugal; *pob*, postorbital; *p*, parietal; *z*, (quadrato-jugal) zygoma; *pg*, pterygoid; *st*, (squamosal) supratemporal; *q*, quadrate. After Cope.

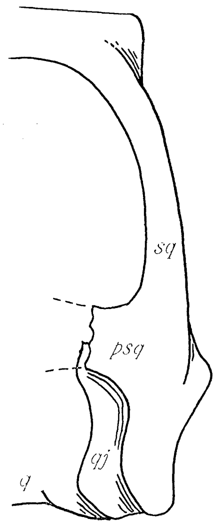

FIG. 5. Edaphosaurus pogonias. Side view of temporal region. *sq*, squamosal; *psq*, prosquamosal; *qj*, quadrate; *q*, quadrato-jugal.

Edaphosaurus pogonias. — This genus differs so markedly from the other Pelycosauria, especially in the presence of a cluster of crushing teeth on the inner side of the mandible, that it may have to be removed from the order. There is one point in the structure, however, that must be mentioned. Cope describes and figures this form (Cope '92) as having but a single arch in the temporal region. In common with most of the other types in the collection this specimen has not been cleaned, and the very slightest removal of the matrix showed that there were two temporal arches instead of one. Instead of the lower portion of the suspensorium being formed of a single mass and connected with a so-called zygomatic bone, as shown by Cope, figure 4, there are several bones, the quadratojugal is broken and crowded under the lower end of the suspensorium, and that there was a distinct process is indicated by a broken stump, which is undoubtedly the posterior end of the prosquamosal arch, figure 5. The position of this arch shows that the upper vacuity was large and rounded and the lower narrow and smaller, perhaps nearly closed, but there were two distinct arches.

Clepsydrops natalis. — The posterior portion of the skull in the type specimen is badly crushed, and the whole specimen is covered with a thin layer of matrix, so that there is much uncertainty regarding the exact limits of each bone. The anterior portion of the skull is strikingly similar to the same region in Dimetrodon and Embolophorus in all the characters of extreme specialization such as the high and narrow facial region, the deep diastema and the enlarged canine and incisor teeth so that there is strong presumptive evidence that the posterior arches had an equal similarity. This is further borne out by the very fact of the fractured condition of the posterior angles of the skull, which are almost universally destroyed in the Pelycosauria because of the weak arches. Certain elements of the temporal region can be made out beneath the thin coating of matrix, but these do not seem to me to be what Cope thought them. He

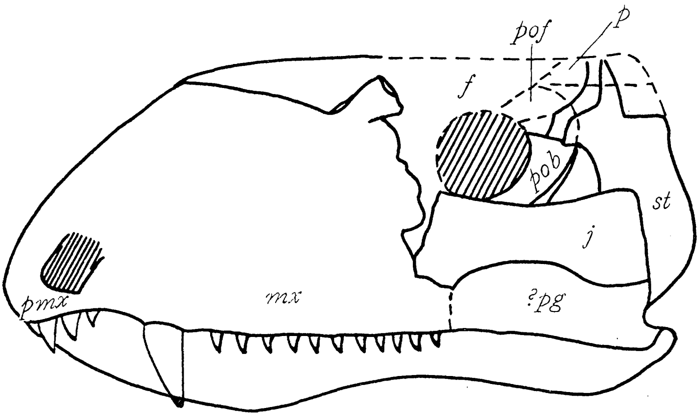

Fig. 6. Clepsydrops natalis. Side view of skull after Cope. *pmx*, premaxillary; *mx*, maxillary; *f*, frontal; *pof*, postorbital; *pob*, postorbital; *p*, parietal; *st*, (squamosal) supratemporal; *j*, jugal; *?pg*, pterygoid.

described and figured but a single arch (Cope '78, '92). The portion marked jugal by him, figure 6, is crossed by a break that seems to me to be very likely along the suture between the quadrato-jugal and the jugal. Posterior to the orbit the bones are badly broken and mixed, but certain parts seem capable of a very different interpretation from that of Prof. Cope. The small fragment labeled post-orbital in Cope's figure seems to me to be a bit of bone from the base of the skull extending out of the orbit. Posterior to the orbit Cope has figured but one piece which he calls the supratemporal; this appears different to me inasmuch as the anterior edge distinctly shows the rounded excavation forming the posterior edge of the orbit and indicating that it is the postorbital bone. Further back the mass bifurcates, this would make the anterior leg of the bifurcation the lower part of the postorbital, a consideration which is borne out by its relation to the upper part of the jugal; the suture between the two is hidden by the matrix and a fracture. The posterior leg is exactly in the position of the anterior end of the postorbital-prosquamosal arch if the arches had the same depressed form as in Dimetrodon. These ideas are expressed in figure 7.

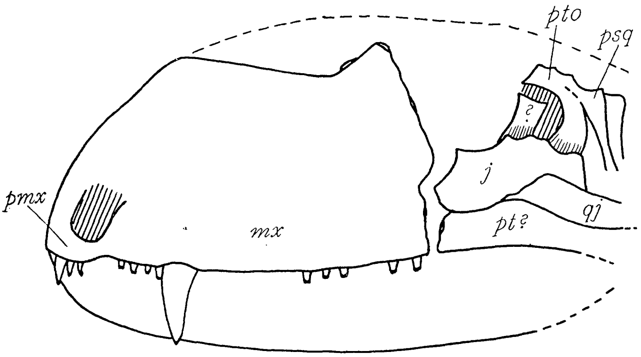

Fig. 7. Clepsydrops natalis. Side view of the skull represented in fig. 6 without any attempt at restoration, as it appears to the author. *pmx*, premaxillary; *mx*, maxillary; *pto*, postorbital; *psq*, prosquamosal; *j*, jugal; *qj*, quadrato-jugal; *? pt*, pterygoid.

Further evidence that Clepsydrops had the same arch structure as in Dimetrodon is found in the greatly elevated neural spines which are found only in the most specialized types. In Clepsydrops they are from eight to nine times the length of the centrum.

For purposes of comparison the figure of the lateral aspect of the skull of Dimetrodon is here introduced to show the most specialized skull of the Pelycosauria. Figure 8.

The relation of the African forms to the American. — Just as the American Pelycosauria passed through a series of specializations which led to extinction so the related African forms (Therosuchia or Therodontia) seem to have passed through a series of stages which promised persistence and which if not leading directly to the ancestry of the mammals at least illustrate by a beautiful example of convergence the method by which the articular region of the mammals might have been developed.

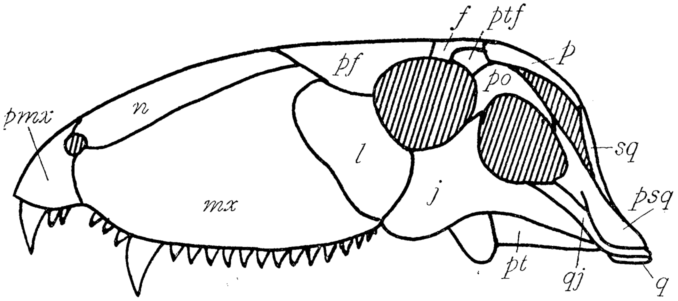

FIG. 8. Dimetrodon incisivus. Side view of skull. *pmx*, premaxillary; *mx*, maxillary; *n*, nasal; *pf*, prefrontal; *f*, frontal; *l*, lachrymal; *ptf*, postfrontal; *po*, postorbital; *p*, parietal; *j*, jugal; *sq*, squamosal; *psq*, prosquamosal; *pt*, pterygoid; *qj*, quadrato-jugal; *q*, quadrate.

The most important steps in the development of the skull structure from a form like Diopeus to such a form as Gomphognathus or Tritylodon seem about as follows:

1. The degeneration to the quadrate and the development of a definite posterior cranial wall by the extension of the parietals.
2. A tendency to the union of the bones of the postorbital and temporal regions to form solid temporal arches.
3. The approximation and union of the two temporal arches to form a zygoma.
4. The union of the posterior end of the zygoma with the prosquamosal portion of the prosquamosal + squamosal and the squamosal portion spreading out as a thin plate closely applied to the skull wall almost at right angles to the zygoma.
5. The development of a mammalian palatal region and a characteristic basipterygoid region from a type similar to Dime-

trodon by the loss of cartilage and the approximation of the posterior portions of the pterygoids and the basioccipital and basisphenoid bones.

6. The development of the bipartite occipital condyle.

Among the American forms there seems to be none which approach the condition of a single zygomatic arch; among the African forms none has been discovered which shows the two temporal arches at all perfectly.[1] The nearest approach to the Rhyncocephalian condition is in Procolophon and Cynognathus, as the structure of these two clearly indicate the previous possession of two arches we may assume the existence of a Diopeus-like ancestor as indicated above.

I select as examples to illustrate the above conclusions Cynognathus, Galesaurus and Gomphognathus because they are the best preserved and described forms and because they are typical of the three fairly distinct groups, the Cynodontia, Lycosauria and Gomphodontia. All of these have the well developed occipital crest and cranial wall, but show the advancing stages of development in the arches and certain changes of importance in the teeth.

In Cynognathus the postorbital and postfrontal have united and developed posteriorly parallel to the jugal. The jugal bar reaches far back and comes in contact with the inferior portion of the united prosquamosal and squamosal (psq + sq) figure 9. The quadrato-jugal is probably crowded beneath the lower end of the psq + sq as indicated below. The union and strengthening of the bones of the two arches is accompanied by an approximation of the two arches leaving only a small inferior temporal vacuity between the two and by the suppression of the quadrate. The psq + sq is described by Seeley (Seeley '95) as a thin plate bent upon itself nearly at right angles, the point of the angle extending outward and forming the posterior angle of the skull. The inner half of this plate, squamosal portion, lies closely applied to the cranial wall, and the outer, prosquamosal portion, forms the posterior part of the upper half of the composite temporal bar. Seeley describes a vertical channel marking the outer side of the angle of the psq + sq persisting downward to the point where the bone expands to cover the quadrate, this groove probably marks the point of union of the squamosal and prosquamosal.

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[1] In all probability Saurosternon, Huxley, possessed the two temporal arches, but it is primitive to the forms discussed in this paper. It may occupy a position similar to Theropleura among the American forms.

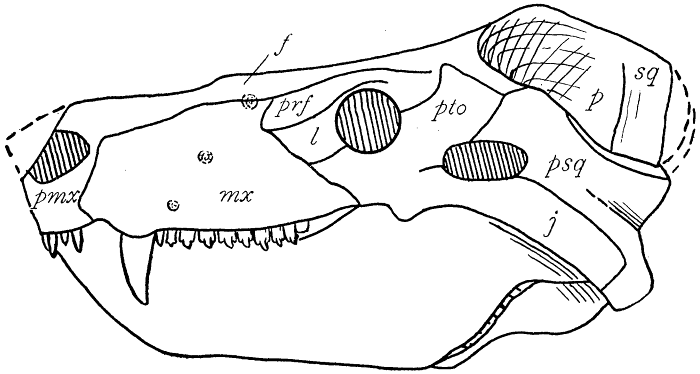

Fig. 9. Cynognathus crateronotus. Side view of skull. *pmx*, premaxillary; *mx*, maxillary; *f*, frontal; *prf*, prefrontal; *l*, lachrymal; *pto*, postorbital; *p*, parietal; *sq*, squamosal; *psq*, prosquamosal; *j*, jugal. After Seeley.

The quadrate is figured by Seeley (figure 10) as a flattened bone with two ascending bars beneath the psq + sq, the two bars show through an evident breaking away of the thin plate of the covering bone. At the same time it is noticeable that the outer part of the lower edge of the psq + sq comes in contact with the articular. Seeley describes the first of the vertical bars as "distinct from the quadrate below and the squamosal above with which it is in close contact"; the same fact is expressed by a line on the quadrate separating the lower part from the portion bearing the vertical bars. It seems very possible that this upper portion is the lost quadrato-jugal which does not appear on the side of the skull.

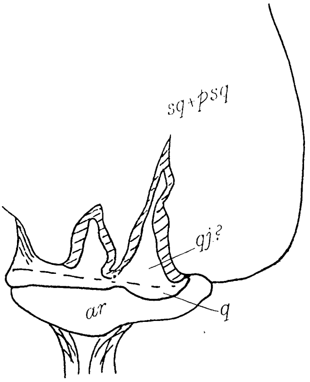

Fig. 10. Posterior view of temporal region of Cynognathus. *sq* + *psq*, squamosal + prosquamosal; *qj?* quadrato-jugal; *q*, quadrate; *ar*, articular. After Seeley.

In Cynognathus the palate is typical reptilian, the teeth have only small lateral tubercles and the whole dentition resembles that of Dimetrodon in the large incisors and canine, the sharp diastema and the convex tooth line.

In Galesaurus and in Cynognathus platyceps there is a single temporal arch with no trace of an inferior temporal vacuity. The bar is formed of two parallel bars, one above the other, with no indication of distinct bones forming each bar. The lower of these bars is called by Lydekker (Lydekker '90) the quadrato-maxillary and the upper the squamoso-maxillary; if the condition of this form is derived from a condition represented by Cynognathus crateronotus the lower bar is really the jugal, the quadrato-jugal having disappeared beneath the psq + sq and the upper bar is the prosquamosal + postorbital. As the prosquamosal is already united with the squamosal, there is now a single mass, the postorbital + prosquamosal + squamosal. Seeley points out that in Galesaurus the lower portion of the psq + sq descends below the quadrate posteriorly.

In Galesaurus the palate approaches the mammalian condition found in the Gomphodontia and the teeth have strong lateral tubercles. The diastema has almost entirely disappeared though there is still a prominent canine.

In Gomphognathus the temporal region is much the same as in Cynognathus, the region is described as follows by Seeley (Seeley '95) "the squamosal rest upon the parietal as a thin film, which descends laterally to the level of the occipital condyles, when it makes a sudden angular bend upward and outward.

The lateral contour of the ascending bar of the squamosal bone is convex, and nearly at right angles to that of the lateral border of the occiput; both are equally thin, and the two plates define a V-shaped squamosal notch which is open superiorly. But the squamosal bone is much more massive than is at first obvious, and below this thin external posterior plate, there is an excavation in the bone, which shows it to be expanded laterally for 1 $\frac{3}{4}$ inch beyond the compressed ridge at the base of the V-shaped fold just described."

The squamosal described by Seeley is of course the psq + sq of this article; the prosquamosal portion forms the posterior part of the zygoma and its anterior end is wedged into the posterior end of the jugal. In front, the edge of the temporal vacuity is formed by the jugal externally and the postfrontal internally. The prosquamosal bar no longer lies parallel to the jugal bar; the jugal bar no longer extends far back to articulate with the prosquamosal near the suppressed quadrato-jugal, but the two bars lie in the same plane and unite in the middle to form a true mammalian zygoma.

In Gomphognathus the mammalian palate is fully developed and the teeth are tuberculated and indicate probably an herbivorous habit.

The significance of the development in the American and African forms.— In a previous paper the author has shown that it is possible to recognize two lines of development in the temporal region of the reptiles. The forms showing the two lines were described as the mastocephalous and saurocephalous groups (Case '98) as follows: "From this point (the Proganosaurian condition, Diopeus[1]) onward the Reptilia are divided into two groups, one with an elongate quadrate, which includes all the modern and most of the extinct Reptilia, and one with a depressed quadrate reaching its highest development in the Permian, and in all probability losing its identity in the direct ancestors of the mammalia." It now seems possible to trace a step farther the origin and history of the phyla.

The lower jaw is the movable element in mastication, and in biting it acts as a lever of the third class with the power supplied by the masseter and temporal muscles applied nearer to the fulcrum, represented by the quadrate, than to the weight, represented by the substance being chewed. It is evident that where the jaws are used for such heavy work as chewing the fulcrum region must be very strong to resist the strain imposed upon it; in the forms which swallow their food without previous mastication, as the Pythonomorpha and Ophidia, and the Amphibia in large measure, there would be little need of resistance in the quadrate region, and in all these forms it is notably weak. The development of a chewing habit, either grinding or sectorial, would bring a greatly increased strain upon this region. We know little that is definite concerning the origin of the temporal and quadrate region in the reptiles next above the Cotylosauria, but as Baur has shown, this may well have developed by a sort of natural trephining of the solid cranial roof, perhaps in response to the demand for a lighter skull connected with changing feeding habits, and resulting in the Proganosauria.[1]

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[1] In the article quoted I stated that the generalized ancestor of the *Pelycosauria* had not yet been discovered, it now seems probable that that stage of evolution is represented by Diopeus, which will be seen from the description given above to fill the necessary conditions.

In the Proganosaurian skull the quadrate was well developed and had much the same position and proportions as in the modern Sphenodon, but was of slightly less vertical extent. As indicated by the character of the teeth these forms used the jaws very little if at all for chewing. The beginning of a chewing habit, either sectorial or the simpler kinds of crushing or grinding, would demand a simple vertical motion of the jaws, with a consequent demand on the quadrate to resist a stronger thrust directed vertically upward. The shape and character of the articular surfaces of the quadrate and articular bones in some of the American forms, as in Dimetrodon, make any other motion than a vertical one impossible.

The strengthening of the temporal and quadrate regions to resist the increased vertical strain was accomplished in two ways: First by an enlargement of the quadrate, especially in the vertical direction, and its closer union with the skull wall; this was accompanied by a decrease in the number of bones in the temporal arches and an enlargement of those remaining (compare the condition in the Squamata and Testudinata). Second by a reduction in the size of the quadrate till it finally disappears (in the mammals or Promammalia) and at the same time a union of the bones of the temporal arches till the articulation of the lower jaw finally comes at the base of a strong buttress formed by the coössified bones of the suspensorium.

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[1] In this connection it is of interest to note that the author discovered perforations in the roof of the skull of the Diadectidæ in the Cope collection in the position of the superior temporal vacuities, the forms are too specialized to make the interpretation of this occurrence certain, but it may well be the first step toward the Proganosauria type. In the line of the argument of this paper it is also interesting to note that the Cotylosauria all had strong, crushing, or grinding teeth and strong quadrate bones firmly enclosed in the roofing bones.

The second of the two processes, described above, was attempted in two different ways. The flattening of the quadrate was common to both, but the supporting temporal arches were disposed of very differently. In the American Pelycosaurians the bones of the temporal arches all retained their identity and remained distinct one from the other, but the posterior ends of the bones followed the quadrate down in its degeneration until the angle of the skull was depressed and the arches were long and slender; compare figures 3 and 8. This made a very weak suspensorium especially as the opisthotic, the single bone which connected the quadrate directly with the skull wall was separated from it by the intervention of considerable cartilage. When the jaw was compressed on food in the act of biting, the strain on the quadrate region would be directly upward, but instead of this strain being met by bones arranged to meet it parallel to their length and firmest attachment, as in the modern lizards, or against bones solidly united and joined to the brain wall, as in the mammals, it was directed almost at right angles against the free ends of slender bones at a point fartherest removed from their attachment to the skull. Such an arrangement was clearly unadapted to resist the strain imposed upon it by the force of the fierce bites these animals were capable of inflicting. As shown above, the advance in the slenderness of the quadrate region kept pace with the advance in the development of the carnivorous habits as evidenced by the increase in size of the incisor and canine tusks and the serrations of the cutting edges of the teeth; the latter speaking of a growing habit of sectorial mastication. The two processes working in opposition.

In the second line of changes that centered around the depressed quadrate there was a decided tendency to a coalescence of the bones of the temporal region; thus the postfrontal and the postorbital were frequently united, the squamosal and prosquamosal the same and the quadrato-jugal either became united with the posterior end of the jugal or, more probably as shown below, disappeared beneath the lower end of the psq + sq. After the union of the individual bones the two arches united, first partially (Cynognathus crateronotus and Procolophon) and finally completely (C. platyceps and Galesaurus). Notable is the position assumed by the squamosal portion of the psq + sq; as shown above in the description of the forms it is spread out as a thin film upon the surface of the cranial wall formed by the developing of the parietals, so that it was firmly held by its application to the skull wall as in the mammalian temporal and is free only at its lower extremity. From this free extremity of the squamosal portion the prosquamosal portion extends forward almost at right angles, the quadrate and quadrato-jugal are probably concealed beneath the point of union of the two and the quadrate is so far overwhelmed that the lower end of the psq + sq comes into articular compact with the articular.

This structure perhaps presents the best mechanism to resist the strain imposed upon the quadrate in biting; it is straight up against the lower end of a bone fastened to the skull by nearly its full length and its parallel to the strongest attachment. That the forms in which it occurs had strongly developed biting habits is evidenced by the tuberculated teeth and the herbivorous grinding teeth of the Gomphodontia.

If the reasoning presented here is correct it is possible to recognize two phyla among the Permian Pelycosauria; one characterized by the persistence of the two Rhyncocephalian arches and the development of a weak articular region, culminating in the high-spined Pelycosauria and the other characterized by the union of the arches and the development of a mammalian temporal region culminating in Gomphognathus and Tritylodon, perhaps in the Promammalia. The last branch practically includes all of the Theriodontia = Theriosuchia.

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